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Racocetra beninensis from sub-Saharan savannas: a new species in the *Glomeromycetes* with ornamented spores

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Abstract — A new fungal species is described under the epithet *Racocetra beninensis* (*Racocetraceae*, *Glomeromycota*). It forms white to creamy-white, globose to sub-globose (sometimes oval) glomerospores terminally on sporogenous cells. Spores measure 195–335 µm diam and have two spore walls: a three-layered outer wall and a three-layered inner wall. The outer spore surface is ornamented with rounded wart-like projections that measure 0.9–2.8 × 0.9–3.8 µm and are spaced (2.2–)4.0–11.0 µm apart. The germination shield that forms on the outer surface of the inner wall is multiple-lobed (6–10 lobes) and (sub-)hyaline or occasionally yellowing with age. The lobes regularly bear a single germ tube initiation. The fungus differs from other *Racocetra* species by spore size and color, ornamentation type, and outer spore wall staining reaction. It has been frequently recovered from sites under natural vegetation and newly cultivated or post-harvest yam (*Dioscorea* spp.) fields in the sub-Saharan Sudan and Guinea savannas of Benin (West Africa).

Key words — arbuscular mycorrhizal fungi, *Gigasporaceae*, *Scutellospora*

Introduction

Arbuscular mycorrhizal fungi (AMF) appear particularly prevalent in tropical savannas (e.g. Sieverding 1989; Tchabi et al. 2008, 2009), where species

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representing the sub-order *Gigasporineae* sensu Morton & Benny (1990) appear most abundant (Maia & Trufem 1990, Oehl et al. 2007, Mathimaram et al. 2007, Goto et al. 2009). In a recent study of AMF diversity of sub-Saharan West Africa, for example, a high diversity of species belonging to *Gigasporineae* J.B. Morton & Benny were recovered from soils in natural savannas and newly cultivated yam (*Dioscorea* spp.) fields (Tchabi et al. 2008). Several of these species have since been transferred to the newly established family *Racocetraceae* Oehl et al. (Oehl et al. 2009), including some regarded as new species (Tchabi et al. 2009). One such undescribed species was first cited as *Scutellospora* sp. WAS1 in Tchabi et al. (2008) and later as *Racocetra* sp. WARa1 in Tchabi et al. (2009). This species, which presented a unique spore wall structure consisting of a conspicuous warty surface ornamentation, is herewith described under the name *Racocetra beninensis*.

Material and methods

Study area and sites

Soils were sampled from 27 natural, fallow, and cultivated sites, located within the Sudan (SU), Northern Guinea (NG), and Southern Guinea savanna (SG) ecological zones in Benin, sub-Saharan West Africa. The climate follows a gradient from SG through NG to SU of decreasing annual rainfall and an increasingly long dry season from 5 to 8 months (Tchabi et al. 2008). The SG has two wet and two dry seasons per annum, while NG and SU are monomodal. The vegetation consists of trees, shrubs and grasses with tree and shrub prominence decreasing from south to north (e.g. Adjakidje 1984, Adjanohoun 1989, Tchabi et al. 2008). The soils are dominantly ferruginous Ferralsols. The selected sites were either natural savannas or yam fields established in the first year after (forest) savanna clearance, mixed cropping systems, groundnut and intensively managed cotton. Sites located in long-term fallows (≥7 years old) were also included to compare species present in undisturbed sub-Saharan savannas with those present in restored fallows and under varying levels of cropping intensification and soil disturbance.

Soil sampling and culturing of AM fungi

Soils were sampled as described in Tchabi et al. (2009) towards the end of the 2004 wet season in September/October and during the subsequent dry season in February 2005. Soil pH, organic carbon, and available phosphorus were determined using standard methods (Tchabi et al. 2008, 2009).

The spore material used for this study derived from field samples. Extensive attempts were made to propagate the AMF species present in the field samples through 'bait' cultures with various hosts (e.g., *Brachiaria humidicola* (Rendle) Schweick., *Stylosanthes guianensis* (Aubl.) Sw., *Sorghum bicolor* (L.) Moench, *Dioscorea cayenensis* Lam., *D. rotundata* Poir). Several bait culture systems were established (Tchabi et al. 2008, 2009) inoculating 5–10% field soils to autoclaved substrate (Terragreen: Quartz sand mixture; 3:1 [wt/wt]). The AMF communities were cultivated for 8–24 months and the host plants periodically analyzed for mycorrhizal infection and AMF spore formation.

The 'bait culturing' resulted in the reproduction of 45 AMF species from ~250 pots, but the species described below was not reproduced (Tchabi et al. 2009). Thus, the present species description is restricted to morphological analyses of spores recovered directly from field samples.

Morphological analyses

Glomerospores extracted from field soils by wet sieving and sucrose centrifugation (Brundrett et al. 1994) were mounted in PVLG, PVLG + Melzer's reagent, and water (Spain 1990, Brundrett et al. 1994). Terminology used in the species description and spore denomination follows Oehl et al. (2009) and Goto & Maia (2006) respectively.

Spore wall ornamentation was compared with that observed in spores in type specimens of other *Racocetra* species; the six species examined were *R. coralloidea* (Trappe et al.) Oehl et al. 2009 [holotype OSC #31'026; paratype OSC #31'025], *R. gregaria* (N.C. Schenck & T.H. Nicolson) Oehl et al. 2009 [holotype OSC #36'518], *R. intraornata* B.T. Goto & Oehl 2009 [holotype URM 79247; isotype OSC #134'506, Z+ZT Myc 775], *R. minuta* (Ferrer & R.A. Herrera) Oehl et al. 2009 [IBACC isotype 7 Herrera/Ferrer-HAC], *R. persica* (Koske & C. Walker) Oehl et al. 2009 [holotype OSC #45'837], and *R. verrucosa* (Koske & C. Walker) Oehl et al. 2009 [holotype OSC #45'838; paratype OSC #45'846].

Taxonomy

Racocetra beninensis Oehl, Tchabi & Lawouin, **sp. nov.** Figs. 1–12

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Sporocarpia ignota. Sporae singillatim in solo efformatae anguste adiacetae ad cellulas sporogeneas subterminales vel intercalares, albae ad ochro-albae, globosae (210–320 µm in diametro) vel subglobosae vel ovales (195–280 × 220–335 µm); sporae tunicis duabus: tunica exterior stratis tribus, in totum 6.5–13.2 µm crassa; stratum exterius tunicae exterioris hyalinum, semi-persistens ad persistens, 1.2–2.2 µm crassum, cum verrucis rotundibus vel ovalibus, 0.9–2.1(–2.8) µm × 0.9–3.8 µm, (2.2–)4.0–11.0 µm in distancia; stratum medium laminatum, album ad ochro-album, 4.5–11.0 µm crassum; stratum interius tunicae exterioris album ad ochro-album, 0.7–1.4 µm crassum; tunica exterior flavum vel fusco-flavum (ad flavo-fuscum) colorans reagente Melzeri; tunica interior de novo formans stratis tribus hyalinibus; tunica interior tribus stratis, 5.4–8.7 µm crassa in totum; tunica interior non colorans reagente Melzeri; scutellum germinale in superficie exteriore tunicae interioris, hyalinum ad subhyalinum ad albo-flavum; ovale vel ellipsoidum vel ovoidum, 95–135 × 110–150 in diameter, lobatum, paucioribus (6–10) lobis depressionibusque germinationis; structurae mycorrhizarum et cellulae auxiliares ignotae. Holotypus: 85-8501 (Z+ZT Myc 1627).

Type: 85-8501 (Z+ZT Myc 1627, **holotype**) from soil samples of a natural savanna in the Southern Guinea Savanna (SG) in Savè, Benin (07°45'74"N; 02°27'52E).

Etymology: *beninensis,* referring to the country in West Africa where the species was first recovered.

Glomerospores are singly formed in soils terminally on a sub-terminal or intercalary bulbous suspensor cell (= 'sporogenous' cell; Figs. 1–2). Glomerospores are white to light ochre, occasionally becoming a light cream colour with age, globose (210–320 µm in diameter) to sub-globose, infrequently

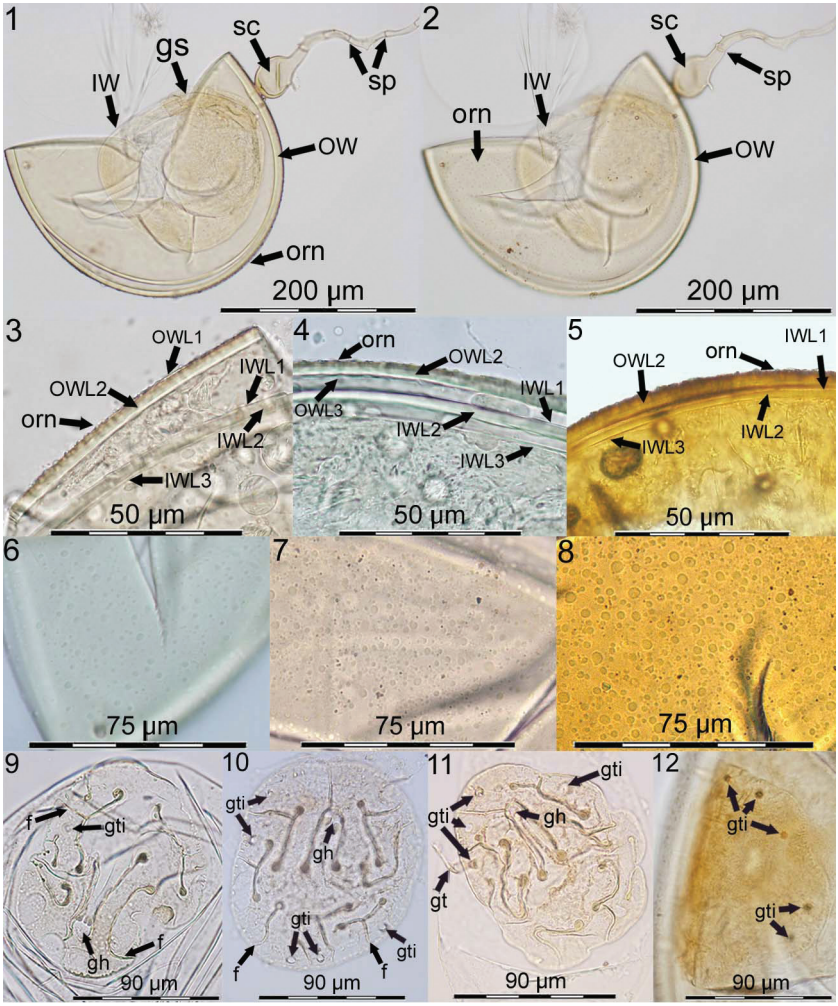
oval (195–280 × 220–335 µm) and have two walls: an outer and an inner wall (OW and IW; Figs. 1–5). Sporocarp formation is unknown.

OUTER WALL is white to light ochre-white, occasionally becoming light creamy with age, in total 6.5–11.0 µm thick and consists of three layers (OWL1–3; FIGS. 3–7). Outermost layer (OWL1) is hyaline to sub-hyaline, semi-persistent to persistent and 1.2–2.4 µm thick (FIGS. 3–4). The outer surface is adorned with wart-like projections that are 0.9–2.1(–2.8) long, 0.9–3.8 µm wide, rounded to oval in planar view and (2.2–)4.0–11.0 µm apart (FIGS. 3–8). The second layer (OWL2) is white to light ochre-white, sometimes becoming light cream when old, 4.5–11.0 µm thick (FIGS. 3–4). OWL3 is concolorous with OWL2, or slightly lighter in color, 0.7–1.4 µm thick but often difficult to observe as closely adherent to laminate OWL2 (FIGS. 3–5). OWL1 may stain light yellow to yellow in Melzer's reagent while OWL2 and OWL3 readily stain bright yellow to dark yellow to yellow-brown in Melzer's (FIGS. 5, 8). The straight pore channel on the OW at the connection with the sporogenous cell is about 3.1–5.5 µm broad and often closed by a plug formed by spore wall material of OWL2, but sometimes appears to be open.

INNER WALL is three-layered (FIGS. 3–5) bearing a germination shield on the outer surface (FIGS. 1–2, 9–12), 5.4–8.7 µm thick in total. Outer layer of the inner wall (IWL1) is hyaline, semi-flexible to unite and 1.2–2.4 µm thick. Second layer (IWL2) is finely laminate, 2.8–5.5 µm thick. Innermost layer (IWL3) is 0.9–1.5 µm thick, (semi-)flexible and, as it tends to tightly adhere to IWL2, can be difficult to detect. The three layers may slightly expand in PVLG based mountants. The IW does not stain in Melzer's reagent.

SPOROGENOUS CELL (SC) is formed terminally or intercalary, globose to elongate, concolorous with the spore, or occasionally bright yellow to yellow brown in older spores, 37–56 µm long and 34–48 µm in diameter (FIGS. 1–2). Two wall layers are generally visible on sc being continuous with OWL1 and OWL2. OWL1 on the sporogenous cell is 0.7–1.4 µm and semi-persistent; persistent OWL2 is 2.2–3.9 µm thick. Warty-projections were never observed on sc surface. The sporogenous cell hypha attached is 12–20 µm broad and also bi-layered, tapering to 5–9 µm within 200–350(–500) µm distance from sc. The sporogenous hyphal wall is concolorous with the sporogenous cell wall, sometimes lighter yellow in color, and tapers from 1.2–2.2 µm to 0.9–1.4 µm within this distance. Several (3–8) septa originating from the inner layer (OWL2) may be visible in the hypha (FIGS. 1–2).

GERMINATION SHIELD is hyaline to sub-hyaline (FIGS. 9–11), infrequently light yellow in aged spores (FIG. 12), oval to ellipsoid or ovoid, 95–135 × 110–150 µm in diameter, and generally has 6–10 lobes (FIGS. 8–10), which are difficult to differentiate when the shield is not readily observed in planar view (FIG. 12).



Figs. 1–12. *Racocetra beninensis.* Figs. 1–2. Spore with sporogenous cell (sc), two walls (ow and iw), a germination shield (gs) on iw, and a wart-like ornamentation (orn) on the surface (Fig. 2). Sporogenous hypha with several septa (sp). Figs 3–5. Spore wall structure in cross view with three-layered ow (owl1-3) and three-layered iw (iwl1-3); ow stains yellow brown in Melzer's reagent (Fig. 5). Figs. 6–8. Wart-like projections on ow in planar view, variable in size and distance between each other; ow dark yellow in Melzer's (Fig. 8). Figs. 9–12. Multiple-lobed germ shields in various developmental stages. Fig. 9. Young shield with initial germ hole (= germ pore); germ tube initiations (gti) still barely visible; large folds (f) separate the lobes. Figs. 10–11. Mature shields with several gti in focus, from where 1–2 germ tubes (gt) emerge during germination. Fig. 12. Old shield of a degrading spore; shield contents slightly darkened; gti significantly darkened and clearly visible.

Large folds (~10–50 µm long) arise from the shield wall separating the lobes (Figs. 9–12). The one-layered shield wall and the folds are hyaline to subhyaline and generally only 0.8–2.1 µm thick. Each lobe may bear one rounded germ tube initiation (gti, Figs. 9–12), 2.9–5.5 µm in diameter. The gti may remain undetectable in young spores (Fig. 9), becoming increasingly visible with age of spores, being easily observed in mature spores (Figs. 10–12).

Spore development — The key stages of spore development could be deduced from clearly identified spores of *R. beninensis*, recovered from soil sampled from the field on different occasions. First the outer spore wall differentiates into one evanescent to semi-persistent outer layer (owl1) with its randomly dispersed, wart-like projections, the laminate layer (owl2), and the adherent thin inner layer (owl3). The three-layered inner wall (iw) develops de novo without visible connection with the outer wall. Finally, the germination shield differentiates its multiple-lobed structure, beginning from the initial germ hole (= germ pore) and forming a gti at the end of the shield development in each of the lobes; from there the germination tubes emerge during initial germination.

Germination — One to two germ tubes may arise. They are light yellow to bright yellow, 5–7 µm in diameter and emerge from one or two gti's (Fig. 11). Germ tubes directly penetrate the ow and branch then almost immediately in the soil environment. The mono- to bi-layered germ tube walls are ~1.2–2.0 µm thick in close spore vicinity.

Auxiliary cells — unknown.

Mycorrhiza formation — unknown.

Distribution — *Racocetra beninensis* is so far known only from sub-Saharan savannas of Benin. The new fungus was found at 13 of 27 total collection sites, including 8 (of 10) natural savanna vegetation sites, 4 (of 5) yam fields, and one (of 3) fields cropped to mixed maize and groundnut (Table 1). It was not recovered from the 3 monocropped groundnut field soils cultivated in the third year of continuous cropping, the 3 intensively managed cotton fields in the fourth year after forest clearance, or from the 3 7-year old fallows (Tchabi et al. 2008). Geographical locations and selected soil physico-chemical parameters of the 13 productive sites are given in Table 1.

Additional specimens examined: **BENIN. Southern Guinea Savanna (SG). Savè:** Isotype specimens (85-8502, 85-8503, 85-8504, 85-8505, 85-8506) deposited at Z+ZT (Z+ZT Myc 1627), **BENIN. Southern Guinea Savanna. Okpara:** paratype specimens (85-8507, 85-8508) deposited at OSC (OSC #134,713); **BENIN. SG. Ikoko:** paratypes (85-8511, 85-8512) deposited at Z+ZT, paratypes (85-8521, 85-8522) deposited at FB (Freiburg, Germany); **BENIN. SG. Zogbodomey:** paratypes (85-8523, 85-8524) deposited at URM. Further paratype specimens from 13 sites of SU, NG, and SG (Table 1).

Table 1 Geographic and soil data for *Racocetra beninensis* isolation sites

Ecological Zone Sampling sites	Geographic location	pH (H_2O)	Organic C g kg^{-1}	Available phosphorus mg kg^{-1}	
				(Na-Acetate)	(Citrate)
Sudan Savanna					
Natural Savanna 1	10°56'N; 01°32'E	6.1	13.9	47.6	69.9
Natural Savanna 2	10°08'N; 01°56'E	6.5	23.8	3.9	8.7
Yam field 1	10°08'N; 01°51'E	5.9	11.6	3.9	8.7
Maize&groundnut mix	10°19'N; 01°35'E	6.2	6.4	7.4	13.1
Northern Guinea Savanna					
Natural Savanna 3	08°43'N; 02°40'E	6.6	9.3	8.7	8.7
Natural Savanna 4	09°03'N; 02°04'E	6.7	36.0	46.3	65.5
Southern Guinea Savanna					
Natural Savanna 5	07°46'N; 02°28'E	6.7	9.9	14.8	34.9
Natural Savanna 6	07°57'N; 02°26'E	7.2	13.9	8.7	13.1
Natural Savanna 7	07°35'N; 02°19'E	6.4	13.9	28.4	43.6
Natural Savanna 8	08°20'N; 01°51'E	6.5	20.3	28.8	34.9
Yam field 2	07°49'N; 02°15'E	6.1	9.3	8.7	8.7
Yam field 3	07°55'N; 02°11'E	6.7	16.8	10.9	13.1
Yam field 4	08°20'N; 01°51'E	6.2	6.4	6.5	8.7

Racocetra species with ornamentations on the spore surface

Five other *Racocetra* species have spore surface projections (Table 2). The spores of these species are more heavily pigmented — yellow to yellow-brown or orange-brown, to red-brown to dark brown to black (Figs. 13–21, Table 2; Gerdemann & Trappe 1974, Nicolson & Schenck 1979, Ferrer & Herrera 1981, Koske & Walker 1985). Moreover, in *R. coralloidea*, *R. gregaria*, *R. verrucosa*, and *R. persica* the spore surfaces are densely crowded with variously shaped and sized papillae or wart-like projections (Figs. 13–20, Table 2). In *R. minuta*, the projections have a central depression on the apex (Ferrer & Herrera 1981, Fig. 21).

Discussion

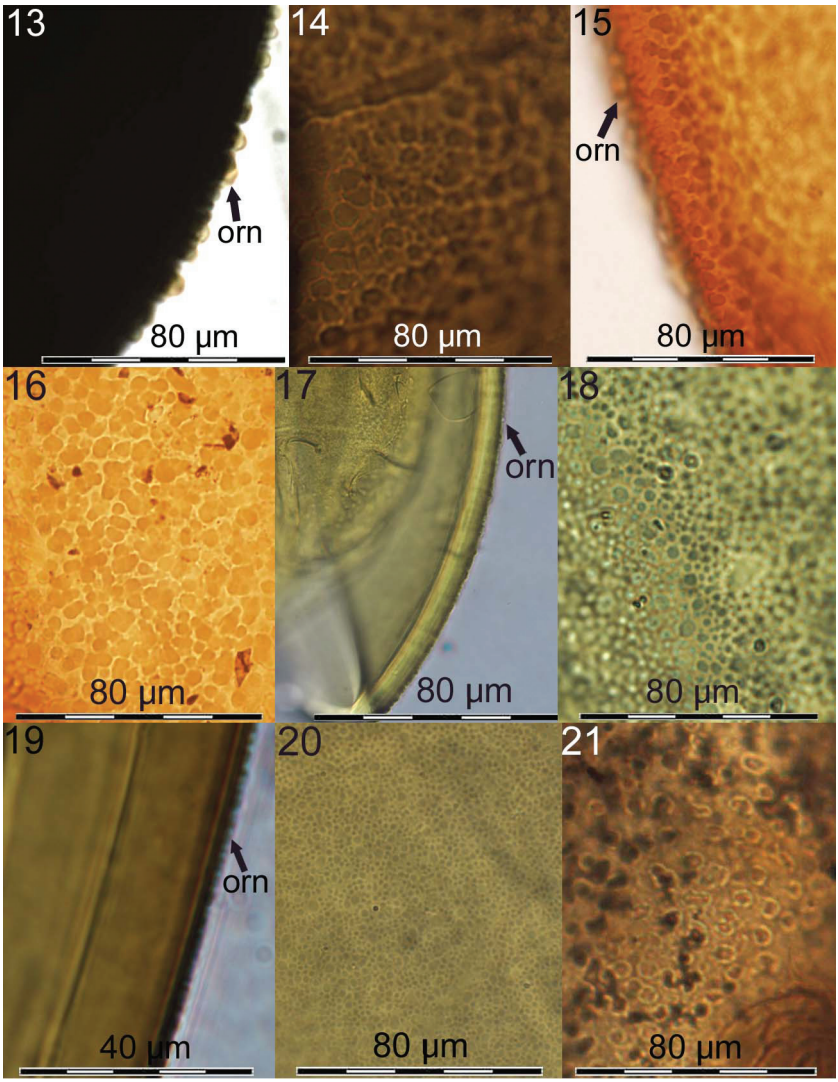
Racocetra beninensis is easily distinguished from all other known species in the genus by spore size and color, ornamentation type, and the different outer wall (ow) staining reaction. The ten species attributed to *Racocetra* are characterized by bi-walled spores and a multi-lobed, hyaline to rarely light yellow germination shield on iw and, as far as it is known, by a more or less intensive ow staining reaction in Melzer's (Table 2; Oehl et al. 2009). Four species lack ornamentation: *R. fulgida* (Koske & C. Walker) Oehl et al.,

Table 2 Spore characters in *Racocetra* species with projections on the spore outer wall (OW) surfaces

Species	Spore size (µm)	Spore color	Outer Wall: Thickness; Color in Melzer's	Projections (µm): Diam. × height [Distance between]
R.beninensis	195–280 × 220–335	White to light ochre	6.5–11 µm; Bright yellow to yellow brown	0.9–3.4 × 0.9–2.5 [(2.5)4.5–11]
R.coralloidea	300–400 × 320–460	Very dark brown to black	8–15 µm; Black	0.5–6 × 1.5–2.5 [0.5–2.0]
R. gregaria	250–450 × 250–480	Dark brown to dark red-brown	6–9 µm; Dark brown	3–12 × 1–10 [0.5–1.8]
R.minuta	95–180	Dark brown to opaque	5.5–8.5 µm; Unknown	1.9–3.0 × 2.5–3.9 [4.0–6.0]
R.persica	270–360 × 280–390	Pinkish orange to brown-orange	2.5–11 µm; Dark red-brown	0.4–0.6 × 0.3–0.6 [0.5–1.0]
R.verrucosa	220–480 × 220–480	Straw yellow to orange-brown	5–16 µm; Dark red-brown	0.5–1.5 × 0.5–1.5 [0.5–1.5]

R. castanea (C. Walker) Oehl et al., *R. alborosea* (Ferrer & R.A. Herrera) Oehl et al., and *R. weresubiae* (Koske & C. Walker) Oehl et al. (Ferrer & Herrera 1981, Koske & Walker 1986, Walker et al. 1993, Oehl et al. 2009). One species, *R. intraornata*, has tuberculate projections on the inner ow surface (Goto et al. 2009). The remaining species (i.e., *R. coralloidea*, *R. gregaria*, *R. minuta*, *R. persica*, *R. verrucosa, R. beninensis*) are all characterized with projections on the outer spore surface (Figs. 11–19, Table 2). In *R. persica,* the surface of the pinkish-orange to brown-orange spores is crowded with fine papillae (Koske & Walker 1985), while the surfaces of the brown *R. gregaria* and almost black *R. coralloidea* spores are densely crowded with rounded or coralloid warts (Gerdemann & Trappe 1974, Nicolson & Schenck 1979, Koske & Walker 1985, Oehl et al. 2009). *Racocetra verrucosa* is distinguished by its (straw) yellow to yellow-brown spores that are crowded with wart-like projections that are usually smaller than those in *R. gregaria* and *R. coralloidea* but more prominent than in *R. persica* (Koske & Walker 1985, Oehl et al. 2009). Beside *R. beninensis*, only *R. minuta* has spores that are not densely packed with projections on the outer surface. However, their brown spores have regularly sized, equidistant projections that have conspicuous central depressions at their apex (Ferrer & Herrera 1981). Finally, *R. beninensis* is similar in color (white to creamy white) with only *R. fulgida*, which does not display any ornamentation.

In the new species a short peg often forms on the sporogenous cells (Figs. 1–2). We interpret such pegs as aborted hyphae but have called this type of sc formation intercalary. As the hyphae never exceeded 15–20 µm in length,



Figs. 13–21. Types of spore surface ornamentation in *Racocetra* (cross and planar views). Figs. 13–14. *R. coralloidea*. Figs. 15–16. *R. gregaria*. Figs. 17–18. *R. verrucosa*. Figs. 19–20. *R. persica*. Fig. 21. *R. minuta*.

we do not know whether they continue as branching mycelial hyphae or form another sc a short distance from the previous, as seen in *Gigaspora ramisporophora* Spain et al. 1989.

Racocetra beninensis was regularly recovered from natural sub-Saharan savannas in all three ecological zones surveyed in Benin. It also frequented yam fields during the first year after savanna clearance but was less frequent in traditional maize/groundnut mixed cropping systems in the second year of agricultural production. The fungus was not observed or recovered from field soil later in the cropping cycle, i.e. the rhizosphere of traditionally grown groundnut or from intensively managed cotton fields.

The fungus did not appear to restore during long-term fallows that followed the 5–7-year agricultural cycle (Tchabi et al. 2008). In conclusion, along with several other species of the *Gigasporineae* (e.g. *Scutellospora calospora* (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders 1986 and *Cetraspora pellucida* (T.H. Nicolson & N.C. Schenck) Oehl et al. 2009; Jansa et al. 2002, Oehl et al. 2003, 2005), *R. beninensis* appears negatively affected by soil disturbance mediated through agricultural intensification. Its existence may consequently be seriously threatened in the sub-Saharan tropics through intensifying agricultural practices caused by increasing land pressure.

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